

## ON THE AFFINITIES OF CÆNOLESTES.

[MARSUPIALIA].

BY R. BROOM, M.D., C.M.Z.S., Corresponding Member.

In 1895, Oldfield Thomas described the remarkable South American marsupial, *Cænolestes*; and gave reasons for believing that it represented a new type of Diprotodontia, and apparently a living representative of a group previously known by a few extinct forms.

With regard to its affinities, Thomas considered that it is closely allied to none of the living forms, but that it is more nearly related to the existing marsupials of Australia, than to those of America. "It is," he adds, "clearly a Diprotodont, as not only does it possess the characteristic development of the lower incisors, but even the molars resemble most closely in structure those of certain members of the family *Phalangeridae*, while being wholly unlike those of the typical Polyprotodonts. From all of the existing Diprotodonts, however, apart from its habitat and numerous detailed differences, *Cænolestes* is at once distinguished by its not being syndactylous, a character which is always considered as of family rank. It forms, therefore, among existing Marsupials a peculiar Family, and one which in America represents the Diprotodonts of Australia, just as the *Didelphyidae* do the Polyprotodonts."

In 1896, I had an opportunity, through the kindness of Mr. Thomas, of examining the type-skull; and I then came to the conclusion that *Cænolestes* was much more nearly allied to the American Polyprotodonts than to the Australian Diprotodonts. When dealing with the affinities and habits of *Thylacoleo*, in a paper published in 1898, I gave a diagram of what I regarded as the phylogenetic relationships of the

Diprotodonts: and, in connection therewith, I stated "*Cænolestes* has been omitted, as I consider the evidence which would place it with the Australian Diprotodonts not sufficiently strong, and in any case it is evidently not a near ally of any of the Australian forms."

Most recent authors seem to have accepted *Cænolestes* as a primitive, but true Diprotodont. In October, 1909, however, a paper was published by Miss Pauline H. Dederer, in which she compares *Cænolestes* with known Polyprotodonts and Diprotodonts.\* She shows that *Cænolestes* exhibits many Polyprotodont characters, and only very few Diprotodont; and her conclusions may be given in her own words. "Sinclair concluded that *Cænolestes* is very like the primitive Phalangiers, and the two families are probably related, not convergent; that, while the fossil *Cænolestidæ* are too specialised in tooth-structure to be the direct ancestors of the Phalangiers, yet there is probably a common ancestry. Later, he gave weight to the possibility of convergence to account for the resemblance in tooth-structure. This latter view would seem to be more in accord with the facts known about *Cænolestes*, for excepting tooth-structure, there appears to be no other important character which links it with the Diprotodonts, and there are several, as given above, which link it with the Polyprotodonts. While there is undeniably a series of forms connecting *Cænolestes* with the Diprotodonts in tooth-structure, yet *Cænolestes* itself is so generalised in this respect, that we may perhaps, in the absence of other corroborating characters, question its inclusion within this group. Possibly it may be found to be an offshoot from the Polyprotodonts, as it appears structurally to be more generalised than any Diprotodont, and, therefore, it might well occupy a separate suborder, as Thomas suggested—the *Paucituberculata* of Ameghino." Thomas had suggested that a further knowledge of the soft parts, skeleton, and milk-

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\* American Naturalist, xliii., 614.

teeth might necessitate the separation of *Cænolestes* from the Diprotodonts, and the placing of it and its fossil allies in a distinct suborder.

Gregory, in his most important work on the orders of mammals, accepts Miss Dederer's conclusion, and places *Cænolestes* in a separate suborder—the Paucituberculata—equivalent to the suborders Polyprotodontia and Diprotodontia. In the diagram he gives of the phylogeny of the marsupials, he derives the Cænolestoids quite independently of the Phalangeroids from a generalised Polyprotodont which lived in Upper Jurassic times.

It is admitted by all that *Cænolestes* resembles the Diprotodont in only two points, which, as stated by Miss Dederer, are—"(1) Condition of teeth: (a) one large lower incisor, cutting, projecting forward; (b) other incisors and canine in lower jaw vestigial as in Epanorthidæ; (c) anterior premolars small, showing tendency towards condition seen in Phalangers, where they are vestigial. (2) Pattern of teeth—molars like Phalanger molars rather than the Polyprotodont type."

On the other hand, Miss Dederer gives a list of ten Polyprotodont characters shown by *Cænolestes*, though one of those given, the equality of the fore and hind limbs, is of little importance, and had better be omitted. The remaining Polyprotodont characters are:—

"(1) Dental formula like that of the Dasyurid genera *Thylacinus*, *Phascologale*, namely:  $i. \frac{4}{3}$   $c. \frac{1}{1}$   $pm. \frac{3}{3}$   $m. \frac{4}{4}$ ; in this family, the incisors are numerous, small, subequal; canines larger than incisors. This agrees with the condition in the upper jaw of *Cænolestes*."

"(2) Close resemblance in external form to *Phascologale*—rat-like or opossum-like in form (Thomas)."

"(3) Resemblance to *Dasyurus* skull, (a) in general shape, (b) pterygoid processes of palatine slender and delicate, (c) alisphenoid bullæ similar in general form."

“(4) Marked resemblance to *Antechinomys* and *Sminthopsis* skulls in size, shape, and delicate character of the bones; absence of strong crests or ridges.”

“(5) Palate long and narrow, similar to characteristic Polyprotodont form, with long and narrow palatal vacuities.”

“(6) Lower jaw very similar to *Dasyurus*, *Phascologale*, and especially to *Antechinomys* and *Sminthopsis* in inflection of angle, and proportionate size of angle, condyle, and coronoid.”

“(7) Rudimentary pouch (Thomas, after *Tomes*), as in *Phascologale* and *Marmosa*.”

“(9) *Pes non-syndactyl*, as in *Dasyures* and opossums.”

“(10) Foot plantigrade—resembles *Phascologale* in number and position of pads, and short clawless hallux (Thomas).”

While one or two of these characters may not, in themselves, have very much weight in determining affinities, most of them are of great importance; and the assemblage of these numerous Polyprotodont characters in one animal makes the case so strong in favour of a Polyprotodont affinity, that only the presence, on the other hand, of very strong Diprotodont characteristics would suffice to outweigh them.

The more one goes into detail, however, the more striking does the Polyprotodont affinity become; and, in addition, to the characters noted by Miss Dederer, the following others may be mentioned.

Unfortunately the soft parts are not known, but there is reason to believe, from the structure of the bones, that the arrangement of the nasal cartilages is much more typically Polyprotodont than Diprotodont. The turbinal springs, as in Polyprotodonts from low down on the nasal wall. The nasal floor is also, as in Polyprotodonts, a wider groove than in Diprotodonts. Further, the arrangement of the palatine processes of the premaxillæ is also typically Polyprotodont.

The structure of the tympanic region is, in every detail, typically Polyprotodont, and quite unlike the condition in any Diprotodonts. The tympanic bone is a slender ring,

which is protected by a well developed, thin alisphenoid bulla. An exactly similar condition is found in the Didelphids, and a somewhat similar condition in the Dasyurids and Peramelids. The arrangement of the foramina in the squamosal bone, and the relations of the squamosal to the periotic are all typical Polyprotodont characters.

In the relationships of the bones, and the foramina in the posterior basicranial region, *Cænolestes* closely resembles the primitive Didelphids, such as *Marmosa*, and less closely the Australian Polyprotodonts; while the differences from the conditions in the Diprotodonts are considerable.

Apart from the condition of the teeth, *Cænolestes* is a typical Polyprotodont in all its cranial characters, and the question to be considered is whether the Diprotodont-like character of the teeth is of sufficient weight to place *Cænolestes* among the Diprotodonts, in spite of the cranial characters all pointing in the other direction.

Now while a type of dentition may remain practically unaltered throughout long ages, if the habit remains the same, it is surprising how readily the type may be altered with change of habit. Thus in the Didelphids we find a dentition which has remained with little change throughout the Tertiary period. But the Diprotodonts of Australia, though closely related, have, in probably a very much shorter time, evolved in a number of very different ways. Further, numerous instances can be given of animals in no way nearly related to each other, evolving closely similar types of dentition. For example, take the molars of *Notoryctes* and *Chrysochloris*, or of *Diprotodon* and *Dinotherium*. And a Diprotodont arrangement has been independently evolved in a large number of the mammalian orders, *e.g.*, Multituberculata, Rodentia, Ungulata, Primates, Chiroptera, and even to some extent in the Insectivora.

Though in *Cænolestes* the dentition bears a superficial resemblance to that of the Diprotodonts, it really differs in some important points. In the first place, no known Dipro-

dont has more than three incisors; *Cænolestes* has four. In Diprotodonts, the canine, though often present, is always of less importance than the incisors; in *Cænolestes*, the upper canine is larger than the incisors. The molars undoubtedly are more like those of the Diprotodonts than the Polyprotodonts: but when we look at the molars of some of the bandicoots, we see that *Cænolestes* is not so very far removed from known Polyprotodont types: and the last two molars seem still to retain a considerable amount of Polyprotodont character. The lower first incisors are undoubtedly developed to a degree quite unknown in any Polyprotodont, but we find a tendency to the increase of the first incisors in a number of Polyprotodonts. In *Phascologale*, it is so well marked, that this genus might be looked upon as incipiently Diprotodont, the first incisor both above and below being much longer than the other incisors, and nearly as large as the canines.

Miss Dederer, Dr. Gregory, and Sinclair, while agreeing that *Cænolestes* should not be placed in the Diprotodontia, prefer to place it in a distinct suborder, the *Paucituberculata*. But it has long seemed to me that, as *Cænolestes* differs from the typical Polyprotodonts only in tooth-specialisation, it should not be removed from the Polyprotodontia, but merely be made the type of a distinct family, or section at most. If the acquirement of a diprotodont dentition is to lead to an animal's being placed in a distinct suborder, then *Chiromys* must be removed from the Prosimiæ, and *Desmodus* from the Microchiroptera.